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Morphological Differentiations between Subspecies in *Arisaema thunbergii* (Araceae) with Special Reference to Sexual Dimorphism

Takahiro OMORI[a], Jenn-Che WANG[b] and Jin MURATA[a]

[a]Botanical Gardens, Graduate School of Science, The University of Tokyo, Hakusan 3–7–1, Bunkyo-ku, Tokyo, 112-0001 JAPAN;
[b]Department of Life Science, National Taiwan Normal University, Taipei, 11718 Republic of China

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In *Arisaema thunbergii* Blume, two Japanese subspecies, subsp. *thunbergii* and subsp. *urashima* (H. Hara) H. Ohashi & J. Murata, and subsp. *autumnale* J. C. Wang, J. Murata & H. Ohashi, recently described from Taiwan, have been recognized. Morphological variations in *A. thunbergii* between these subspecies are examined with special reference to sexual dimorphism and are discussed here in order to characterize each subspecies more clearly. We observed natural populations of subsp. *autumnale* in Taiwan and examined the number of leaflets and the length of peduncle, petiole, rachis, and terminal leaflet using dried specimens of all the subspecies. Differences between sexes were recognized in the peduncle/petiole length ratio in all subspecies. The degree of difference was most extreme in subsp. *autumnale*. The Taiwanese subsp. *autumanale* could be distinguished from the other subspecies in every character examined, while Japanese subspecies showed some similarities in leaf morphology and dissimilarities in peduncle length to each other. The differences in morphology and flowering season may suggest that the Taiwanese subspecies is a distinct species.

Key words: *Arisaema thunbergii* subsp. *autumnale*, morphology, sexual dimorphism.

Arisaema thunbergii Blume, a tuberous perennial plant, had long been considered indigenous to Japan and Chejudo Island of Korea (Ko and Kim 1985). *Arisaema thunbergii* is widely distributed in the temperate forest zone of the Japanese archipelago from southwestern Hokkaido to the Tokara Islands. Ohashi and Murata (1980) recognized two subspecies in the species, that is, subsp. *thunbergii* and subsp. *urashima* (H. Hara) H. Ohashi & J. Murata, the latter of which is sometimes treated as a distinct species (*A. urashima* H. Hara). Their distributional areas slightly overlap each other: subsp. *thunbergii* is distributed in western Japan to the west of Wakayama Prefecture and Chejudo Island, while subsp. *urashima* is found in central and eastern Japan to the east of Chugoku District and disjunctively in Fukuoka Pref., Kyushu. Subsp. *thunbergii* and subsp. *urashima* can be distinguished by the morphology of the base of spadix-appendage, which is inflated and wrinkled in subsp. *thunbergii*, and cylindrical and smooth in subsp. *urashima*.

About a decade ago, *A. thunbergii* was reported from Taiwan, and was initially treated as subsp. *urashima* (Wang 1992). Recently, Wang (1996) confirmed that its chromosome number is equal to the other two subspecies

(2n = 28), while recognizing it as a new subspecies based on its autumnal flowering period, and differences in the morphology of pollen and spathe (subsp. *autumnale* J. C. Wang, J. Murata & H. Ohashi).

An important characteristic of *Arisaema* is the phenomenon of sex change. Several studies demonstrated that sex expression in the genus changes according to plant size (e. g., Kinoshita 1986, 1987, Takasu 1987). The length of peduncles is known to increase during sex change to female in some taxa (e. g., *A. heterocephalum* Koidz.), and vice versa (e. g., the *A. undulatifolium* group). Such morphological shifts accompanied by sex change have often been used as an important taxonomic indicator for this genus (Ohashi and Murata 1980, Murata 1986, Kobayashi et al. 2000), or interpreted as a consequence of different reproductive strategies in each sex (Lloyd and Webb 1977, Kinoshita 1986). This phenomenon of shifting sexual dimorphism is therefore important not only in a taxonomic, but also evolutionary context.

Murata (1986) reported the ranges of variation in the length of peduncle and petiole in many taxa, including *A. thunbergii*, but subsp. *autumnale* was unknown at that time. Our field observation in the autumn of 2003 revealed that Taiwanese subspecies had more distinct characteristics, especially in sexual dimorphism, than previously recognized (Wang 1992, 1996).

Here we study the morphology of all the three subspecies of *A. thunbergii*, with special attention to sexual dimorphism in subsp. *autumnale*. We aim to characterize each subspecies more clearly and discuss their taxonomic status.

Materials and Methods

In the autumn of 2003, the senior author visited eight populations of subsp. *autumnale* in Taiwan, and observed 144 living plants including 31 males and 12 females. The number of leaflets, the size of peduncle, petiole, rachis, and terminal leaflet were examined on dried specimens collected at that time and also those deposited in the Herbarium of Institute of Botany, Academia Sinica, Taipei (HAST), the Herbarium of Kyoto University (KYO), the Herbarium of The University of Tokyo (TI), and the Herbarium of the Department of Biology, National Taiwan Normal University (TNU).

Analysis of Variation (ANOVA) and Least Significant Difference method (LSD) was conducted to confirm the significance of differences in the averages among taxa.

Results

Number of leaflets (Table 1, Fig. 1a)

In subsp. *autumnale*, leaflet numbers per leaf ranged from 11 to 15 and usually from 7 to 11, but rarely to 15, based on Wang (1996) and Gusman and Gusman (2002). In this study, the variation range was from 7 to 12 in males, and from 9 to 12 in females, and no significant difference was found between sexes.

In subsp. *thunbergii* and subsp. *urashima*, leaflet number in male plants ranged from 9 to 20 and from 9 to 19; those in females from 11 to 23 and from 11 to 21, respectively. These results are concordant with Takasu's (1987), who extensively studied natural populations of subsp. *urashima*. Significant difference between sexes was found in each subspecies ($p < 0.001$).

Both Japanese subspecies often have 13 leaflets or more, but we could never find any plant of subsp. *autumnale* that had less than 13 leaflets per leaf. In contrast to other subspecies, the averages of subsp. *autumnale* were significantly lower, irrespective of sex ($p < 0.001$). The Taiwanese subspecies is distinct from others in the number of leaflets.

Length of rachis (Table 1, Fig. 1b)

The length of rachis generally increases in females from that in males. Significant

Table 1. Measurement of morphobogical characters in *Arisaema thunbergii*

	subsp. *thunbergii*	subsp. *urashima*	subsp. *autumnale*
Male			
Number of leaflets			
average (± sd)	13.4 (± 2.57)[a]	13.4 (± 2.32)[a]	9.53(± 1.07)[c]
range (number of samples)	9–20 (36)	9–19 (95)	7–12 (30)
Length of rachis (cm)			
average (± sd)	10.8 (± 3.02)[a]	9.56 (± 3.47)[a]	5.42 (± 2.55)[d]
range (number of samples)	5.2–21 (34)	2.5–19 (92)	2.9–9.2 (6)
Length of terminal leaflets (cm)			
average (± sd)	16.6 (± 3.46)[a]	15.6 (± 3.28)[a]	14.1 (± 3.60)[a]
range (number of samples)	11.3–26.7 (35)	8–23 (89)	9.8–21.9 (9)
Length of petiole (cm)			
average (± sd)	28.9 (± 6.13)[a]	28.4 (± 7.47)[a]	25.4 (± 6.04)[a]
range (number of samples)	17.7–42.5 (21)	12.5–43.6 (66)	19–37.3 (10)
Length of peduncle (cm)			
average (± sd)	7.59 (± 2.93)[a]	12.7 (± 2.99)[b]	16.2 (± 3.02)[d]
range (number of samples)	2.2–14 (21)	7.1–18.5 (65)	12.2–21.3 (10)
Peduncle length/petiole length ratio			
average (± sd)	0.26 (± 0.095)[a]	0.46 (± 0.11)[c]	0.65 (± 0.064)[d]
range (number of samples)	0.12–0.45 (21)	0.26–0.92 (65)	0.55–0.74 (10)
Female			
Number of leaflets			
average (± sd)	15.7 (± 2.83)[b]	15.7 (± 2.04)[b]	11.0 (± 0.43)[c]
range (number of samples)	11–23 (20)	11–21 (37)	10–12 (12)
Length of rachis (cm)			
average (± sd)	16.1 (± 5.45)[b]	12.9 (± 4.62)[c]	12.6 (± 3.94)[a, b, c]
range (number of samples)	7.0–25.5 (20)	5.5–25 (35)	9.6–18.2 (4)
Length of terminal leaflets (cm)			
average (± sd)	21.7 (± 4.02)[b]	19.8 (± 4.77)[b]	29.4 (± 3.24)[c]
range (number of samples)	14.5–29 (20)	9.4–29.6 (31)	25.1–33.6 (6)
Length of petiole (cm)			
average (± sd)	35.6 (± 9.98)[b]	34.6 (± 8.87)[b]	42.7 (± 12.2)[c]
range (number of samples)	20–60.5 (19)	17.3–49.9 (27)	126.5–57.8 (7)
Length of peduncle (cm)			
average (± sd)	6.54 (± 2.30)[a]	9.83 (± 2.41)[c]	10.5 (± 2.92)[b, c]
range (number of samples)	3–12 (19)	4.5–14 (28)	7.4–14.9 (7)
Peduncle length/petiole length ratio			
average (± sd)	0.19 (± 0.076)[b]	0.29 (± 0.073)[a]	0.25(± 0.036)[a, b]
range (number of samples)	0.098–0.44 (19)	0.18–0.49 (27)	0.19–0.29 (7)

a–d: Different letters indicate significant difference by LSD method based on ANOVA ($p < 0.05$).

differences were found between sexes in all taxa (subsp. *thunbergii*: $p < 0.001$, subsp. *urashima*: $p < 0.001$, subsp. *autumnale*: $p < 0.01$). Each subspecies, however, showed its own tendency, probably related to the pattern of arrangement of leaflets (Ohashi and Murata 1980, Murata 1984, Gusman and Gusman 2002).

Although no significant difference was found between subsp. *thunbergii* and subsp. *urashima* in males, there was a significant difference in females ($p < 0.01$; avr. = 16.1 cm, and 12.9 cm, respectively). On the other hand, subsp. *autumnale* was not significantly different from other subspecies in females, but in males was significantly shorter than subsp. *thunbergii* ($p < 0.01$) and subsp. *urashima* ($p < 0.05$).

Length of terminal leaflet (Table 1, Fig. 1c)

The average terminal leaflet lengths of subsp. *thunbergii*, subsp. *urashima*, and subsp. *autumnale* were 16.6 cm, 15.0 cm, 14.1 cm in males, and 21.7 cm, 19.8 cm, 29.4 cm in females, respectively. As in length of rachis, the averages of terminal leaflet length of female plants were significantly higher than those of males in subsp. *thunbergii* ($p < 0.05$), subsp. *urashima* ($p < 0.001$), and subsp. *autumnale* ($p < 0.001$). Subsp. *autumnale* was distinctive in that the variation range never overlapped between sexes.

The two Japanese subspecies did not significantly differ from each other, while subsp. *autumnale* had significantly higher values than any other subspecies in female plants ($p < 0.05$).

Length of petiole (Table 1, Fig. 1d)

In petiole length, the averages of subsp. *thunbergii*, subsp. *urashima*, and subsp. *autumnale* were 28.9 cm, 28.4 cm, 25.4 cm in males, and 35.6 cm, 34.6 cm, 42.7 cm in females, respectively. The length of petiole of female plants were significantly higher than those of males in subsp. *thunbergii* ($p < 0.05$), subsp. *urashima* ($p < 0.001$), and subsp. *autumnale* ($p < 0.001$). As in length of terminal leaflet, the variation range scarcely overlapped between sexes in subsp. *autumnale*.

Although subsp. *thunbergii* and subsp. *urashima* did not significantly differ from each other, subsp. *autumnale* had significantly higher values than any other subspecies in female plants ($p < 0.05$).

Length of peduncle (Table 1, Fig. 1e)

In contrast to the leaf characters mentioned above, two Japanese subspecies could be distinguished from each other in the sexual dimorphism of this character: in subsp. *thunbergii*, no significant difference was found in the average peduncle length between males and females (avr. = 7.59 cm, 6.54 cm, respectively), while difference was distinct in subsp. *urashima* ($p < 0.001$; avr. = 12.7 cm, 9.83 cm, respectively) and in subsp. *autumnale* ($p < 0.001$; avr. = 16.2 cm, 10.5 cm, respectively).

Significant differences were also found among taxa in both males and females. The averages of subsp. *thunbergii* were the lowest in both sexes. That of subsp. *autumnale* was significantly higher than any other subspecies in males ($p < 0.001$) and than subsp. *thunbergii* in females ($p < 0.01$). No significant difference, however, was found between subsp. *urashima* and subsp. *autumnale* in females.

Ratio of the peduncle/petiole length (Table 1, Fig. 1f)

Our results are consistent with the well-known fact that all subspecies of *A. thunbergii* have peduncles shorter than the petiole (Ohashi and Murata 1980, Murata 1984, Wang 1992, 1996). The averages in subsp. *thunbergii*, subsp. *urashima*, and subsp. *autumnale* were 0.26, 0.46, 0.65 in males, and 0.19, 0.29, 0.25 in females, respectively. It has already been reported that the values for female plants were significantly lower than those of males in *A. heterocephalum* Koidz., *A. negishii* Makino, and *A. sikokianum* Franch. & Sav. (Ohashi and Murata 1980, Murata 1986). In *A. thunbergii*, significant differences were also found between males and females in all subspecies: subsp. *autumnale* ($p < 0.001$), subsp. *urashima* ($p < 0.001$), and subsp. *thunbergii* ($p < 0.05$).

Compared with intersubspecies differences in females, those in males could be clearly recognized. In male plants of subsp. *urashima*, difference between the maximum (= 0.92) and minimum value (= 0.256), and standard deviation was considerable. This may be due to the large sample size.

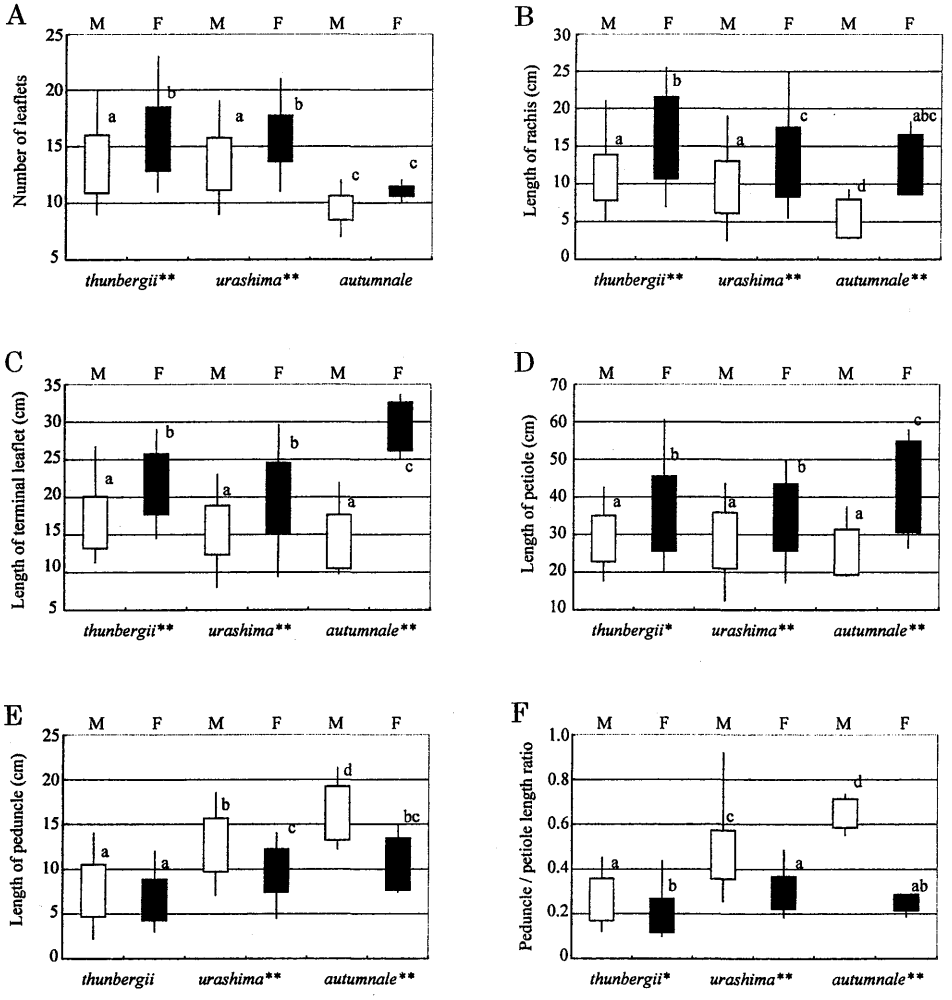

Fig. 1. Diagrams illustrating the ranges in the three subspecies of *Arisaema thunbergii* A: Number of leaflets. B: Length of raches. C: Length of terminal leaflets. D: Length of petioles. E: Length of peduncles. F: Length ratio peduncle/petiole. Both ends of solid lines indicate maximum and minimum values; open and solid bars indicate the average ± standard deviation ranges of males and females, respectively. The alphabets, a–d, correspond to those in Table 1. Asterisks labeled in the end of subspecific epithets, * and **, represent that the subspecies show sexual differentiation at 0.05 and 0.001 level, respectively.

Habitat of subsp. autumnale

Arisaema thunbergii is typically found at the edge and within evergreen or deciduous forests in Japan. Through our field observation, we encountered large populations of subsp. *autumnale* mainly on light slopes around streams in the low mountains, where they seemed to experience intermittent disturbances by heavy rainfall. We could not find them where interspecific competition would be high, even if other conditions appeared to be convenient to subsp. *autumnale*. We consider that such places may be their primary habitats.

Discussion

Differentiation between sexes: Sexual dimorphism

For leaf morphological characters such as length of rachis, terminal leaflet, and petiole, the averages of females were higher than those of males in all taxa. These results are quite natural, considering that nutritional conditions determine sex expression in this genus.

For length of peduncle, difference was recognized between sexes except for subsp. *thunbergii*: the averages of females were significantly higher than those of males in subsp. *urashima* and subsp. *autumnale*. Differences in peduncle/petiole length ratio between sexes were seen in all taxa.

These results suggest a general tendency in *A. thunbergii*: peduncles will, more or less, shorten through feminization, converse to petioles. Kinoshita (1986) pointed out the possibility that sexual selection causes sexual dimorphism in some Japanese *Arisaema* species. For example, robust peduncles in females will have the advantage of ensuring seed maturation, and longer ones in males may be adaptive in pollen dispersal, or male-male competition (Kinoshita 1986). Further study is required to verify whether this hypothesis would match our results directly or not, but evidently the differences in the extent of sexual dimorphism among the three subspecies will reflect those in their evolution. In that sense, it is interesting that inter-subspecies differences in females were not as large as that in males.

Differentiation among subspecies

It is known that the three infraspecific taxa of *A. thunbergii* are distinct from each other in some characters, such as morphology of spadix-appendage and pollen, distinctness of longitudinal stripes on spathe, and flowering period (Table 2). The two Japanese subspecies are more similar to each other than to Taiwanese subspecies, although they differ in morphology of the spadix-appendage. Both subsp. *thunbergii* and subsp. *urashima* flower in spring. Their stripes are not as distinct as those of subsp. *autumnale* and their pollen grains have spinules with an acute apex. Meanwhile, subsp. *autumnale* has an autumnal flowering period, distinct stripes on the spathe, and pollen grains with obtuse spinules (Wang 1996).

Our results on leaf morphology characterized each subspecies more clearly, and confirmed relative similarities between Japanese subspecies. No significant difference was found between them except that females of subsp. *thunbergii* had significantly longer rachises. By contrast, Taiwanese subspecies had significantly different values in all the characters examined: Subsp. *autumnale* has quite fewer leaflets in both sexes, significantly shorter rachis in males, and longer petiole and terminal leaflet in females. Murata (1984) mentioned, in his extensive study of *Arisaema*, that arrangement of leaflets should be an important indicator of the genus, and determined not only by number of leaflets but also the degree of rachis development.

In peduncle length, subsp. *thunbergii* had significantly lower averages in both sexes than any other subspecies. They did not show differentiation between sexes unlike subsp. *urashima* and subsp. *autumnale*, in which males had distinctly higher values. On the peduncle/petiole length ratio, sexual dimorphism was found in all taxa. As mentioned above, this may be the result of the evolutionary trend that each subspecies has.

Taxonomic consideration of Arisaema thunbergii

Our results demonstrated morphological differentiations among three subspecies and characterized each taxon more clearly. The two Japanese subspecies, subsp. *thunbergii* and subsp. *urashima*, were sometimes distinguished at specific level. However, the dif-

Table 2. Diagnostic characters of infraspecific taxa in *Arisaema thunbergii*

Characters	subsp. *thunbergii*	subsp. *urashima*	subsp. *autumnale*
Distribution	western Japan and South Korea (Chejudo island)	central and eastern Japan and Kyusyu (Fukuoka Pref.)	northeast of Taiwan
Flowering period	spring	spring	autumn (spring)
Base of spadix-appendage	wrinkled	smooth	smooth
Pollen morphology			
Average of pollen diameter (μm)	21.4[a]	18.5[a]	20.9[b]
Length of spinule (μm)	0.3–1.0[a]	1.0–2.0[a]	1–1.3[b]
Apex of spinule	acute[a]	acute[a]	obtuse[b]
Longitudinal stripes			
on spathe-blade	obscure	obscure	distinct
Number of leaflets*			
in males	–	–	few, usually < 13[c]
in females	–	–	few, usually < 13[c]
Length of rachis*			
in males	–	–	short
in females	long	short	intermediate
Length of terminal leaflets*			
in males	–	–	–
in females	–	–	long
Length of petiole*			
in males	–	–	–
in females	–	–	long
Length of peduncle*			
in males	short[c]	intermediate	long
in females	short[c]	–	–
Peduncle / petiol length ratio*			
in males	low	intermediate	high
in females	low	high	intermediate
The degree of sexual dimorphism			
in peduncle/petiole length ratio	obscure	intermediate	distinct

[a]Based on Ohashi et al. (1983). [b]: Based on Wang (1996). [c]: No sexual dimophism was found. *: Characters examined in this study. –: Not significantly different from each other.

ference in the morphology of the basal part of spadix appendage is not always distinct between them. Our results showed both their dissimilarities in peduncle length or peduncle/petiole length ratio, and relative similarities in leaf morphology. For rachis length of female plants, the average of subsp. *thunbergii* was higher than that of subsp. *urashima*.

On the other hand, subsp. *autumnale* could be distinguished from other taxa in every character examined: in males and/or females, the variation ranges were significantly different from other subspecies. Wang (1996) stated that, regardless of its relative similarities with subsp. *urashima*, this Taiwanese subspecies had many distinct characteristics. Above all, they flower in autumn in Taiwan, although their reblooming in spring has been observed when cultivated in the greenhouse of Tohoku University, Sendai (Ohashi personal communication). The differences in both the peduncle/petiole length ratio and flowering period indicate that they can be characterized from their evolutionary trend, besides other morphological differences.

On the basis of the differences mentioned above and summarized in Table 2, we consider that the taxonomical status of subsp. *thunbergii* and subsp. *urashima* is reasonable

but that subsp. *autumnale* may be treated as a distinct species.

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大森崇広[a]，王 震哲[b]，邑田 仁[a]：**ウラシマソウの亜種間における形態的分化**

ウラシマソウ *Arisaema thunbergii* Blume に認められている3亜種，ナンゴクウラシマソウ subsp. *thunbergii*，ウラシマソウ subsp. *urashima*，および近年台湾から報告された，タイワンウラシマソウ subsp. *autumnale* の特徴を明確にするため，現地調査と標本の計測を行い，性転換に伴う変化と亜種間の分化について考察した．葉形態に関する項目（小葉数，葉軸長，頂小葉長，葉柄長）に関しては，タイワンウラシマソウの小葉数を除いて，雌個体で有意に大きな値を示した．これに対して，花梗長，および葉柄長に対する花梗長の比，における雌雄間の差の程度は亜種によって異なり，ナンゴクウラシマソウでは，花梗長の差は認められなかった．

ナンゴクウラシマソウは雌個体で葉軸が長くなる傾向があり，雌個体，雄個体ともに花梗長が短いことが特徴であった．一方，タイワンウラシマソウは，すべての項目で，少なくとも雌雄いずれかは他亜種と有意に異なる値を示し，小葉数が極端に少ないこと，花梗長における顕著な雌雄間分化などの特徴があった．ウラシマソウは，両亜種の中間的な値を示す傾向があったが，小葉数，頂小葉長，葉柄長に関しては，ナンゴクウラシマソウと有意差は認められなかった．タイワンウラシマソウは，テンナンショウ属としては例外的に秋咲きであるなど，他亜種とは異なった特徴をもっていることが知られているが，本研究の結果，形態的な分化が大きく，特に雌雄間の差がはっきりしていることが明らかとなった．

([a]東京大学大学院理学系研究科附属植物園，
[b]台湾師範大学生命科学部)